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MAYFLY GROWTH AND POPULATION DENSITY IN CONSTANT AND VARIABLE TEMPERATURE REGIMES

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ABSTRACT.—The thermal equilibrium hypothesis predicts that aquatic insect body size/fecundity and, consequently, population density and biomass will be maximized in geographic areas or along altitudinal gradients where the thermal regime is optimal with respect to growth and development. Seasonal growth analyses of three mayfly species, combined with detailed thermal descriptions, were used to explore differences in body size and fecundity at three sites with similar elevations but different temperature regimes. Site 1 was located near the upper altitudinal distribution for each species, whereas sites 2 and 3 were located below a deep-release storage reservoir. The temperature pattern at site 1 had rapid seasonal changes, with a short summer and a long, freezing winter. Site 2 demonstrated gradual seasonal changes combined with winter warm and summer cool temperatures. Site 3 was intermediate with respect to seasonal change and winter harshness but had the highest maximum and mean annual temperatures. Mayfly development at site 1 was characterized by slow growth during the summer-autumn period, no growth during the winter, and a rapid increase during the spring-summer period. In contrast, growth at site 2 was continuous throughout the year, including the winter. Growth at site 3 was either continuous across sites or rapid during the spring-summer period, depending on the species. Based upon the interactions among temperature, body size, and metabolic costs, the thermal equilibrium hypothesis was successful at predicting body size and fecundity differences among sites. It was less successful at predicting variation in population density and biomass. Density-dependent and density-independent sources of mortality, including temperature, may interrupt the translation of higher fecundity into higher population density and biomass.

Temperature, because of its influence on metabolism, growth, and reproductive success, is a dominant ecological determinant of the geographical and altitudinal distributions of aquatic insects (e.g., Vannote and Sweeney 1980, Ward and Stanford 1982, Sweeney 1984, Ward 1986). The thermal equilibrium hypothesis (TE) is a conceptual model of the effects of temperature on aquatic insect metabolism, growth, body size, and therefore fecundity (Sweeney and Vannote 1978, Vannote and Sweeney 1980). It predicts that population density, distribution, and stability (Connell and Sousa 1983) are determined by individual reproductive success and will be maximized in geographic areas or along altitudinal gradients where the thermal regime is

optimal with respect to growth, development, and body size. Fecundity, an essential component, but not the only factor defining reproductive success, should decrease in temperature regimes warmer or cooler than optimal. Other factors, which may influence fecundity and may or may not be influenced by temperature, can determine population size and distribution (e.g., egg-hatching success, emergence success, mating success, feeding rates, assimilation efficiency, food quality and quantity, biotic interactions). The TE hypothesis, however, attempts to define the influence of temperature on population size and distribution based only on the effect of temperature on metabolism, growth, and therefore body size/fecundity.

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The objective of this study was to analyze the influence of temperature on the growth and body size/fecundity of three mayfly species and compare these results with population size (density and biomass) data and the predictions of the thermal equilibrium hypothesis. Three sites were chosen on the same river, all with similar elevations but different temperature regimes. Site 1 was located near the upper altitudinal limit for each species, whereas sites 2 and 3 were located in a warmer, more constant thermal regime downstream from a deep-release reservoir. Specifically, we sought to test the following hypotheses: (1) population size and body size will be smaller for each species at site 1 compared with sites 2 and 3; (2) population size will correspond with body size at the same sites (i.e., site-specific ranks of body size and population size should be the same); (3) seasonal patterns of growth will parallel seasonal temperature patterns. Body size/fecundity was compared to examine its ability to explain among-site differences in population size.

Several studies have demonstrated a positive correlation between body size and fecundity in aquatic insects (see Clifford and Boerger 1974, Kondratieff and Voshell 1980, Sweeney and Vannote 1981). Therefore, we assume that larger mayflies produce more eggs compared with smaller mayflies of the same species. We did not attempt to determine, as predicted by the TE hypothesis and numerous other authors, whether an increase in population size is positively correlated with an increase in population stability. Considerable evidence, however, indicates that larger populations are more stable than smaller populations (e.g., smaller populations are more susceptible to extinction).

STUDY SITES AND INSECT ALTITUDINAL DISTRIBUTIONS

The first hypothesis required us to a priori rank the study sites according to how closely they approximated the optimal temperature conditions for the mayflies under investigation. Our ranks were based on the altitudinal distributions of the insects. Because the study sites were located near their upper limits, the unaltered temperature regime at site 1 was considered cooler than the optimum necessary to maximize body size/fecundity. There-

fore, the warmer, dam-impacted sites 2 and 3 were assumed to be nearer the insects' optimal temperature regime. There was no a priori reason to separate sites 2 and 3 with respect to their influence on growth, body size, and population size even though they had very different temperature regimes.

The study was conducted in the Upper Colorado River on the western slope of the Rocky Mountains in the vicinity of Granby Reservoir, a large (666 km³), deep-release storage impoundment. Granby Reservoir is located 38 km northwest of Denver, Colorado. Site 1 was located in a third-order, free-flowing section of the river 4.0 km above the reservoir; sites 2 and 3 were located 0.4 and 4.0 km, respectively, downstream from the dam. Although differentially influenced by stream regulation, all three sites had similar gradients (0.006–0.009), canopy cover, geology, riparian vegetation, and elevation (2,593 m, 2,454 m, and 2,426 m, respectively. (For complete site descriptions see Rader and Ward [1988].)

Three mayfly species were analyzed in this study: *Drunella grandis* (Eaton), *Ephemerella infrequens* (McDunnough), and *Baetis tricaudatus* (Dodds). Ward (1980, 1986) determined the altitudinal distribution of macroinvertebrates, including the mayflies of this study, in the St. Vrain River, a free-flowing stream running from the alpine tundra to the plains on the eastern slope of the Rocky Mountains. Based on his results, site 1 of this study (upper montane zone) was above the altitudinal distribution for *D. grandis* and very near the upper limits for *E. infrequens* and *B. tricaudatus*. All three species exhibited maximum densities at lower elevations in the foothills or plains zones. Even though their altitudinal upper limits appear to be somewhat higher in the Colorado River, probably because of its larger size compared with the St. Vrain River, we concluded that all three study sites were located near the upper altitudinal limit for each of the three mayfly species.

METHODS

Temperature, Growth, and Body Size

Water temperature was measured continuously at each site for 18 months using Ryan 90-day thermographs. Each thermograph was checked against a Wexler hand-held thermometer on a monthly basis and calibrated

prior to placement and following retrieval. Daily mean temperatures were used to calculate annual mean temperatures, annual coefficient of variation, annual degree days, number of days less than 3 C, number of days equal to 0 C, length of spring-summer and summer-autumn periods, and rate of spring-summer increase and summer-autumn decline.

Annual growth rate analyses and general temperature descriptors (e.g., accumulated degree days, mean annual temperature, etc.) cannot explain site-specific variation in aquatic insect body size and fecundity because they average over important seasonal information. Seasonal growth rate analyses combined with seasonal temperature profiles can, however, provide insights into the relationships between temperature, growth, and body size.

Temperature profiles for each site were separated into three periods: (1) spring-summer, (2) summer-autumn, and (3) winter (Fig. 1). The winter period was defined by mean daily temperatures <3 C in order to include the winter warm temperatures at site 2. The end of the spring-summer period/beginning of the summer-autumn period was set at 15 August, based on temperature peaks apparent at sites 1 and 3 (Fig. 1). Therefore, the spring-summer period began when the mean daily temperature exceeded 3 C and ended 15 August. The summer-autumn period began 15 August and ended when the mean daily temperature dropped below 3 C.

Growth, defined as the monthly increase in mean biomass of individuals collected per sampling date, was determined for *D. grandis* and *E. infrequens*. Growth for *B. tricaudatus* was not analyzed because of difficulty in assigning intermediate-sized instars to the correct generation.

Site-specific differences in seasonal growth rates were determined by regressing monthly mean individual biomass estimates against the number of Julian days accumulated over the three separate growth periods (spring-summer, summer-autumn, and winter). A slopes comparison test (analysis of covariance) was used to determine among-site differences in seasonal growth rates. No transformation was necessary because growth was linear over the short seasonal periods.

Population Size and Body Size

Estimates of population density and bio-

mass were based on four Surber samples (0.09²m each, 240 μm mesh) collected monthly across the width of the stream at each site and four artificial substrates. Artificial substrates consisted of clay bricks (23 × 19 × 9.5 cm) that had been in the streams for one month before being sampled. Most of the Surber samples enclosed natural substrate particles similar in size to the artificial brick substrates. Therefore, sampling units from both techniques were combined because the sampling areas were approximately equal. A simple *t* test indicated that the mayfly population means based on Surber samples of natural substrate were not significantly ($P = .63$) different from population means based on the artificial substrate samples. Following identification and enumeration, all nymphs were divided into 0.1-mm size classes, based on maximum head capsule width, and dried at 60 C for 48 hours. Mean annual population biomass was determined by summing biomass estimates for all size classes across all sampling dates. Mean annual population density was determined after summing the number of individuals in each size class at each site. Head-capsule measurements were also used to construct size-frequency plots for life-history determinations, including the number of annual generations produced. Complete life-history information for these species at each site can be found in Rader and Ward (1989).

Female body size (dry weight biomass) of late instars was estimated by taking the mean of the three largest size classes collected from each site. Late mayfly instars have a full complement of mature eggs.

RESULTS

Temperature, Growth, and Body Size

A progressive increase in accumulated degree days and mean annual temperatures was found from site 1 to site 3 (Table 1). Site 1 was characterized by rapid seasonal changes in temperature and a long, freezing (0 C) winter (Table 1, Fig. 1). In contrast, site 2 demonstrated gradual seasonal changes combined with winter warm and summer cool temperatures. Site 3 was intermediate with respect to rates of seasonal change but had the greatest amount of thermal energy (largest number of accumulated degree days, largest maximum temperature, and largest annual mean temperature).

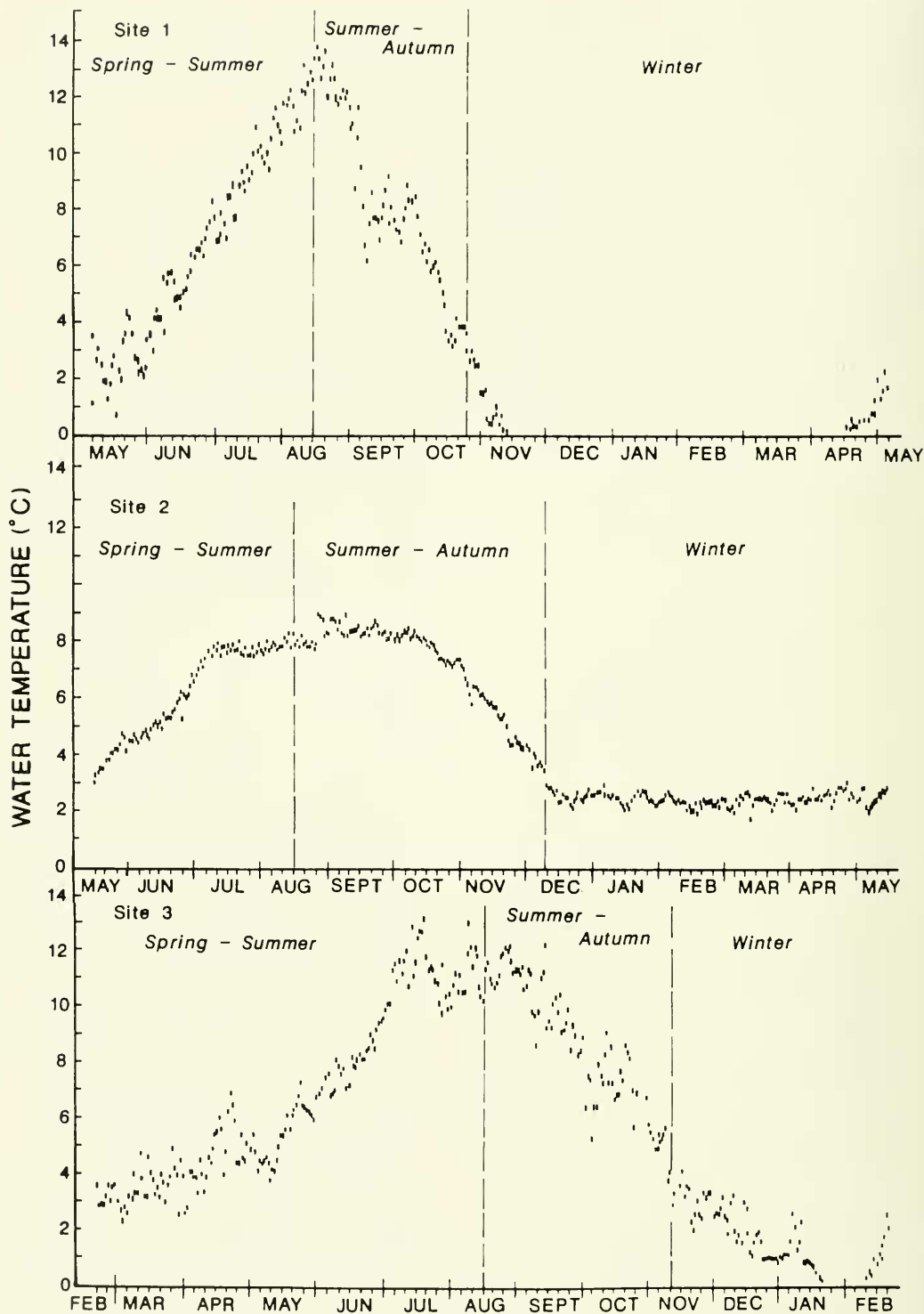


Fig. 1. Temperature profiles for each site during 1981-1982. Individual points represent daily means. (See text for explanation of criteria used to determine seasonal separations. Note that the x-axes have been adjusted to facilitate a comparison of the length of each period at each site.)

TABLE 1. Temperature characteristics of each site.

Characteristic	Site 1	Site 2	Site 3
Annual degree days (C)	1130	1729	2052
Mean annual temperature (C)	3.6	4.7	5.7
C.V. (%)	119	53	64
Minimum (C)	0.0	1.8	0.0
Maximum (C)	18.0	9.8	18.2
Days <3 C	191	155	101
Days = 0 C	153	0	17
Rate of spring-summer ↑ (°C/day)	0.14	0.05	0.06
Length of spring-summer (days)	99	94	177
Rate of summer-autumn ↓ (°C/day)	0.20	0.05	0.10
Length of summer-autumn (days)	70	115	87

Seasonal growth rates were analyzed to explain among-site differences in body size for each species. The seasonal pattern of growth for *D. grandis* and *E. infrequens* at site 1 was characterized by slow growth during summer-autumn, no growth during winter, and a rapid increase during the spring-summer period (Figs. 2, 3). In contrast, growth at site 2 was comparatively fast and continuous through each seasonal period including winter. At site 3, *D. grandis* demonstrated a continuous growth pattern similar to that observed at site 2, whereas *E. infrequens* demonstrated a spring-summer pulsed pattern of growth more similar to that at site 1.

The seasonal growth rate (0.0108 mg/day) for the early instars of *E. infrequens* during the summer-autumn period was significantly ($P = .0001$) faster at site 2 than at sites 1 and 3 (0.004 and 0.003 mg/day, respectively), which were not significantly different (Fig. 2). This trend continued into the winter period when the growth rate at site 2 (0.022 mg/day) was again significantly ($P = .0001$) faster than at sites 1 and 3, where growth rate was not different from zero. By the end of winter, the site 2 population had completed over 76% of its growth, and larvae were over five times larger than those at sites 1 and 3 (Fig. 2). Therefore, the larger body sizes at site 2 can be attributed to rapid growth starting at egg hatch and continuing through the winter. During the spring-summer growth period, individuals at sites 1 and 3 grew significantly ($P = .0001$) faster (0.034 and 0.033 mg/day, respectively) than individuals at site 2 (0.014 mg/day). However, the body sizes of late instar larvae at sites 1 and 3 were still considerably smaller than those at site 2.

The growth rate (0.064 mg/day) of early

instars of *D. grandis* during the summer-autumn period was significantly different among sites ($P = .0001$), being greatest at site 2 and slowest at site 1 (0.035 mg/day). Winter growth was also faster at site 2, with an average rate of 0.064 mg/day, followed by site 3 (0.044 mg/day) and then site 1 (0.015 mg/day). Winter growth at site 1 was not significantly different from zero. Spring-summer growth at site 1, however, was significantly ($P = .0001$) faster than at sites 2 or 3, with the fastest seasonal rate of increase for this study (0.119 mg/day). Spring-summer growth rates at sites 2 and 3 (0.076 and 0.055 mg/day, respectively) were not significantly different.

Baetis tricaudatus was univoltine at site 1, but bivoltine with slow and fast seasonal generations at sites 2 and 3. In contrast, *D. grandis* and *E. infrequens* had univoltine, slow seasonal life cycles at each site. Complete life-history data for each species can be found in Rader and Ward (1989).

As predicted by the first hypothesis, mean annual density and biomass of each species were much greater at the warmer sites below the dam than at site 1 (Table 2). Population density and biomass of *Baetis tricaudatus* and *E. infrequens* were largest at site 2, followed by sites 3 and 1. Maximum density and biomass of *D. grandis* were greatest at site 3, followed by sites 2 and 1.

Contrary to the predictions of the second hypothesis, dry weights of the largest instars, and population sizes of each species, did not correspond when ranked by sites (Table 2). Although the largest late instars of *E. infrequens* occurred at site 2, where the density was greatest, the largest instars of *B. tricaudatus* and *D. grandis* did not occur in the largest population. Body size and population size corresponded in only two other instances; the smallest late instars of *B. tricaudatus* and the intermediate-sized late instars of *D. grandis* occurred in the small- and intermediate-sized populations, respectively, at site 1.

The largest *B. tricaudatus* larvae occurred at site 3, whereas its maximum population density and biomass occurred at site 2. Late *B. tricaudatus* instars at sites 2 and 3 were over two times larger than late instars at site 1 (Table 2). The largest-sized larvae of *D. grandis* occurred at site 2. Site 3, which had the largest population of *D. grandis*, had the smallest late instars (Table 2).

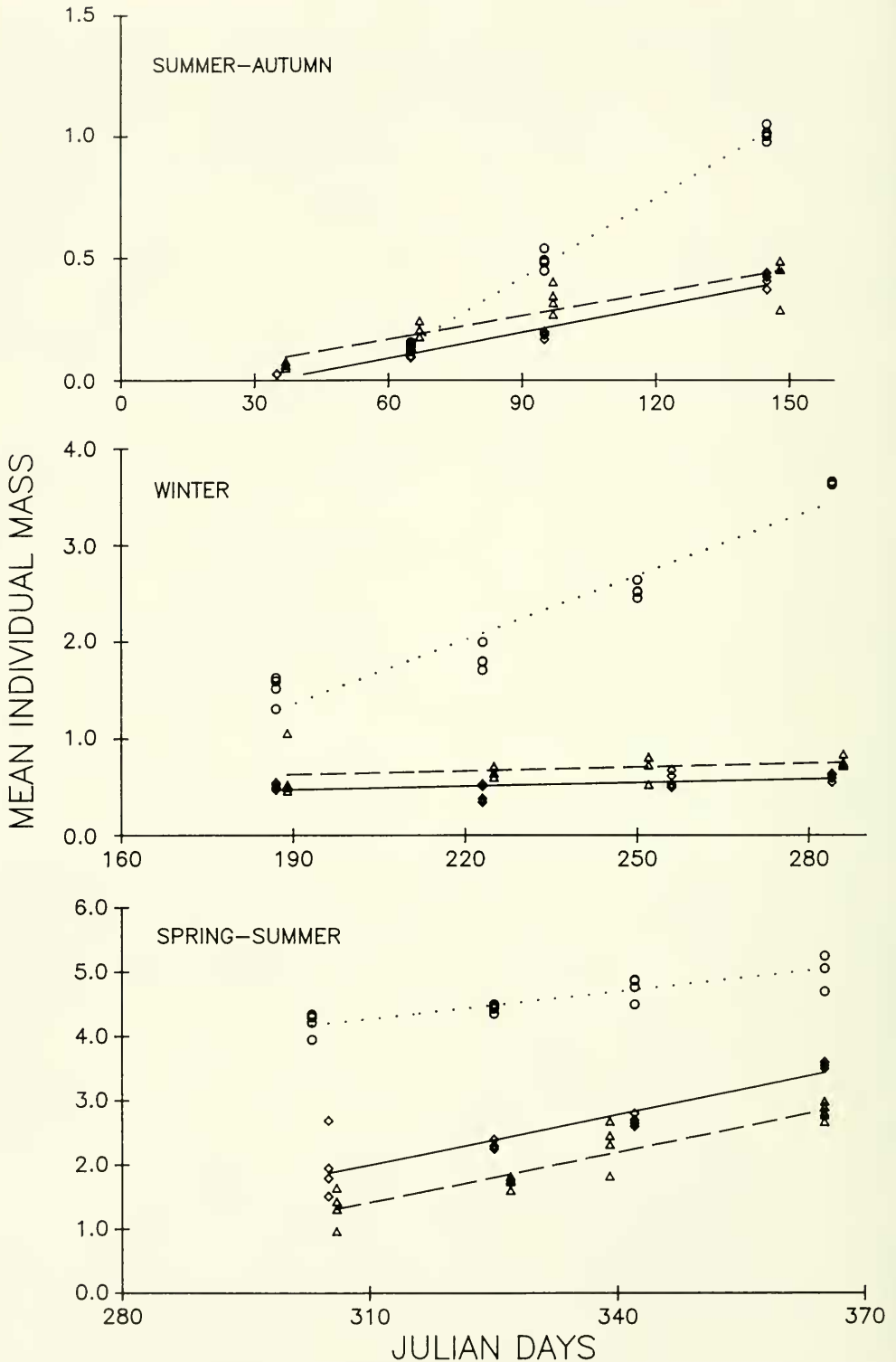


Fig. 2. Seasonal growth rate patterns for *Ephemerella infrequens*. Site 1 is represented by a solid line and diamonds, sites 2 and 3 by a dotted line and circles, and a dashed line and triangles, respectively. Each symbol (diamond, circle, and triangle) represents the mean biomass for a single sample.

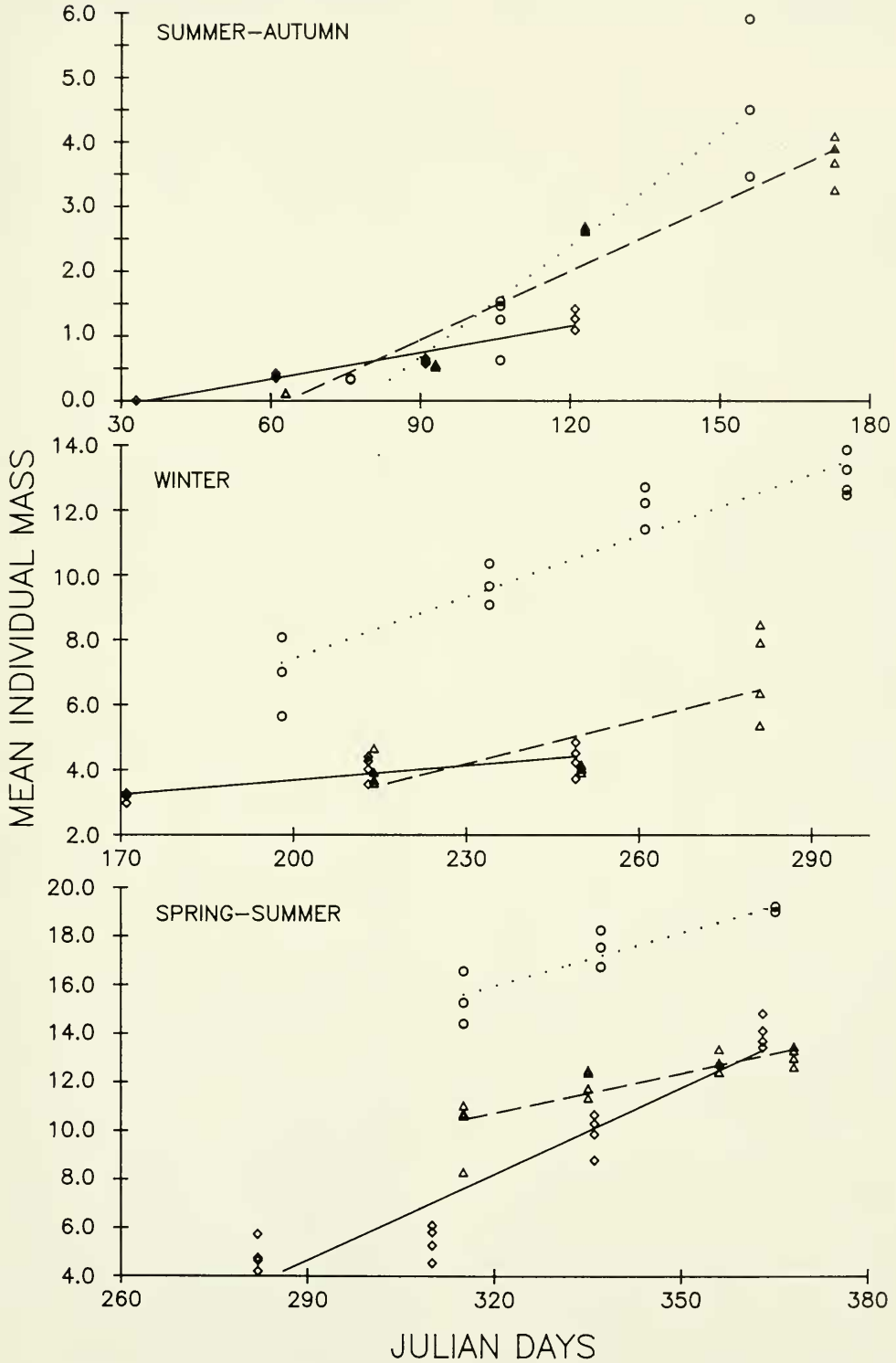


Fig. 3. Seasonal growth rate patterns for *Drunella grandis*. (For further description, see Fig. 2 legend.)

TABLE 2. Mean annual population density ($\# \cdot \text{m}^{-2}$) and biomass (mg m^{-2}), plus mean individual size (mg dry wt.) for late instars of each species. Values in parentheses for the population parameters are the percentage of mean represented by the standard error. Values in parentheses for size estimates indicate the number of individuals used to determine each mean.

Species	Site 1			Site 2			Site 3		
	Population Density	size Biomass	Body size	Population Density	Biomass	Body size	Population Density	size Biomass	Body size
<i>B. tricaudatus</i>	754 (21%)	142.6 (17%)	0.730 (31)	7720 (18%)	1501.7 (21%)	0.550 (35)	4018 (18%)	1162.8 (27%)	1.960 (35)
<i>E. infrequens</i>	367 (25%)	502.6 (23%)	3.500 (23)	1034 (23%)	4964.7 (25%)	4.930 (35)	644 (24%)	1188.5 (26%)	2.800 (25)
<i>D. grandis</i>	102 (31%)	1585.9 (18%)	14.930 (16)	80 (10%)	2368.4 (22%)	18.110 (9)	278 (14%)	3355.4 (20%)	14.220 (17)

DISCUSSION

Temperature, Growth, and Body Size

The winter warm and summer cool conditions of site 2 allowed rapid continuous growth of *E. infrequens* and *D. grandis*, which produced larger instars and greater fecundity. Site-specific explanations of growth patterns and body-size differences for *D. grandis* and *E. infrequens* are consistent with the TE hypothesis. Vannote and Sweeney (1980) proposed that the seasonal pattern of growth for aquatic insects, as for other small ectotherms (e.g., Phillipson 1981), may be determined by the interaction between temperature and body size. Smaller instars, which have a large surface-to-volume ratio, will have a higher metabolic rate than larger instars at the same temperature. At site 1 the smallest *D. grandis* and *E. infrequens* instars appeared during the warmest months of the year (July, August, and September). High summer-autumn temperatures coincident with small instars at site 1 likely resulted in large metabolic costs and, therefore, slow growth rates and possibly high mortality rates. Both species ceased to grow during the freezing winter temperatures. In the spring, winter survivors experienced a rapid increase in temperature and thus a relatively short period (99 days or less) to complete growth and maturation. All else being equal, the magnitude and length of summer-autumn temperatures when coincident with early instars, plus the rate of vernal rise, limit growth and body size/fecundity and probably have an important influence on the geographic distribution and upper altitudinal limits of aquatic insects. This may be espe-

cially applicable to cool-adapted boreal species (see Edmunds 1982).

Early instars at site 2 began growth in much cooler summer-autumn temperatures; metabolic costs were low and growth rates fast compared to those at sites 1 and 3. Winter temperatures, which varied slightly around 2 C, were not sufficiently cold to inhibit growth, which continued at a rapid pace. Growth appeared near completion before the vernal rise in temperature, thus leaving plenty of time for maturation and emergence. The rapid completion of growth probably resulted in the extended emergence of *E. infrequens* and the addition of a second generation of *B. tricaudatus* at site 2.

The early instars of *D. grandis* (July) and *E. infrequens* (August and September) began growth at site 3 during the warmest months of the year. August and September were, on average, 7–8 C warmer at site 3 than site 2. Although *E. infrequens* did not grow, *D. grandis* early instars grew rapidly during the summer-autumn growth period. Because *D. grandis* early instars were approximately two times larger than *E. infrequens* early instars, they probably had lower metabolic costs. This allowed them to grow at the warm summer-autumn temperatures. Although both species stopped growing during winter at site 1 but continued to grow during winter at site 2, only *D. grandis* continued winter growth at site 3. The fact that *D. grandis* was over three times larger than *E. infrequens* at the beginning of winter may explain its ability to grow in winter at site 3 in contrast to *E. infrequens*.

These site-specific explanations of growth are consistent with the TE hypothesis

suggesting that growth rate and consequently body size and fecundity are determined by the length of time individuals are exposed to a specific optimal range of temperatures. Other factors, however, that may also influence mayfly growth rates (e.g., food abundance; Sweeney et al. 1986) were altered by the effects of stream regulation. For example, constant flow conditions and the addition of planktonic diatoms from the reservoir enhanced food quality and quantity at sites 2 and 3 (Rader and Ward 1989).

If summer temperatures increase metabolic costs, causing growth to slow or stop, then the rate of vernal rise and autumn decline determines the amount of time individuals are exposed to optimal temperatures and, therefore, the amount of time available for growth. Growth of both *D. grandis* and *E. infrequens* continued as long as temperatures remained between 2 C and 10 C. However, when temperatures exceeded this range, growth slowed or stopped. Where growth was continuous (site 2), temperatures were always within this range. The optimal temperature range for these two species appears to lie between 2 C and 10 C.

Population Size and Body Size

Winter warm and summer cool conditions at site 2 and the long spring-summer period at site 3 probably accounted for the multivoltine life cycle of *B. tricaudatus* at these sites. Stanley and Short (1988) suggested that population size may remain unaltered or even increase in warmer than optimal conditions if faster growth rates and shorter generation times compensate for smaller body sizes and lower fecundity. For some aquatic insects, warmer than optimal temperatures may offer a trade-off between body size/fecundity and generation time. Will they maximize reproductive effort by producing fewer, larger individuals (slow growth and a univoltine life cycle) or many, smaller individuals (fast growth and multivoltine life cycle)? These data demonstrated that *Baetis* may have the genetic plasticity necessary to respond to such tradeoffs. As temperatures approached optimality (site 2) from cooler conditions (site 1), both voltinism and body size increased within the same population. When comparing site 1 with the much warmer and very different temperature regimes downstream from the reservoir,

we found that our data support the predictions of the TE hypothesis. The largest body size and population size of each species occurred downstream from the reservoir. However, site-specific comparisons of body size and population size did not correspond as predicted by the TE hypothesis. The thermal regimes at sites 2 and 3 were apparently sufficiently similar that temperature did not have an overriding influence on population sizes. The TE hypothesis assumes that higher fecundity is equivalent to larger population size. Sources of mortality at every stage of development, eggs, nymphs, and adults (Sweeney and Vannote 1982, Butler 1984, Peckarsky 1984, Gilliam et al. 1989), which may vary across sites, may interrupt the translation of higher fecundity into higher population density and biomass. Numerous factors, in addition to the influence of temperature on body size/fecundity, will undoubtedly influence the geographic or altitudinal variation in aquatic insect population size and stability. Toward the center, and probably over most of a species range, other sources of mortality and determinants of reproductive success should have a greater influence on aquatic insect population size. Temperature at the edge of a species range may, however, be more limiting, compared to other factors, in determining the extent of a species distribution.

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